

A COMPARISON OF ORCHID FLORAS OF TEMPERATE NORTH AMERICA AND EASTERN ASIA¹

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ABSTRACT

A phytogeographic analysis is made of the orchid floras of temperate North America and eastern Asia. The relationships between them are shown characteristically by the disjunctive patterns of distribution in the eight species-pairs of *Cypripedium*, *Listera*, *Pogonia*, *Liparis*, and *Platanthera*, as well as in some other genera such as *Tipularia*, *Arethusa* (*Eleorchis*), *Aplectrum* (partly *Cremastra*), and *Tropidia*, in the two continents. Data of these distribution patterns support an assumption that the discontinuous distribution in orchids between temperate North America and eastern Asia is the result of migration via the Beringian link, or by way of the northern Pacific, but this was not necessarily the only migration route concerned.

The Orchidaceae is an advanced family with minute seeds that can be dispersed effectively by wind over long distances. Because there are so few nutrients in the seeds, their distribution is restricted by ecological conditions. There are a number of closely related orchids extensively or disjunctively distributed between temperate North America and eastern Asia; among them, species pairs are most interesting. These pairs are similar in morphology to the extent that most previously have been considered as conspecific. Although such morphological similarities do not necessarily indicate genetic relationships, they often do. No attempt is made here to further examine the question of their evolutionary relationship, which would require investigations using other approaches, especially cytogenetic research. The purpose of this paper is to discuss how present distribution patterns have been developed.

FLORISTIC COMPARISON

There is a striking similarity between temperate North American and eastern Asian orchid floras. In the latter area, however, there occurs a large number of taxa, including many endemics and primitive forms.

A total of 106 species with many varieties in 23 genera are reported to occur in temperate North America (Correll, 1950; Luer, 1975), whereas in eastern Asia there are about 350 species grouped into 80 genera, of which 62 genera including 15 species occur in Japan (Ohwi,

1953). Among them, 16 genera are common to both continents: *Cypripedium*, *Cephalanthera*, *Epipactis*, *Listera*, *Pogonia*, *Spiranthes*, *Goodyera*, *Orchis*, *Coeloglossum*, *Platanthera*, *Habenaria*, *Liparis*, *Malaxis*, *Corallorhiza*, *Tipularia*, and *Calypso* (excluding *Aplectrum* and *Arethusa*). Consequently, more than two-thirds of the total orchid genera of temperate North America show a phytogeographic link with eastern Asia. No single genus is found exclusively in North America and Europe, whereas there are several strictly Eurasian genera such as *Neottia*, *Epipogium*, *Herminium*, *Neottianthe*, *Gymnadenia*, and *Peristylis*.

Few epiphytic orchids are found in North America except in southern Florida and coastal and southern Mexico, whereas in China several genera of epiphytic orchids occur south of the Qin Ling Mountains: *Coelogyne*, *Pholidota*, *Pleione*, *Ischnogyne*, *Liparis*, *Dendrobium*, *Eria*, *Oberonia*, *Holcoglossum*, *Cleisostoma*, *Vanda*, and *Taeniophyllum*. Some grow as far north as about 34° to 36°N latitude. Examples are *Liparis fargesii* Finet (33°55'N), *Dendrobium hancockii* Rolfe (33°55'N), and *Cleisostoma scolopendrifolium* (Makino) Garay (36°N) (Chen & Tang, 1982).

High endemism in eastern Asia is notable. Seven genera, *Tangtsinia*, *Diplandrorchis*, *Changnienia*, *Stigmatodactylus*, *Ephippianthus*, *Dactylostalix*, and *Neofinetia* (not including *Eleorchis* and *Kitigorchis*), are confined to eastern Asia, whereas three, namely *Hexalectris*, *Calopogon*, and *Isotria*, occur only in temperate

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North America. In addition, eastern Asia has more subendemic genera such as *Bletilla*, *Hemipilia*, *Porolabium*, *Amitostigma*, *Archineottia*, *Androcorys*, *Ischnogyne*, and *Holcoglossum*. The richness of the above-mentioned eastern Asian orchid flora results in part from the wide range of available areas from subtropical to temperate zones, and a number of tropical taxa that have ranges extending northward into this region. However, in North America and northern Africa there is no such range of areas because of the interruption by either ocean or desert, and few tropical orchids there spread northwards as far as in eastern Asia. Similarly, in eastern Asia temperate genera such as *Cephalanthera*, *Epipactis*, *Listera*, *Pogonia*, and *Hemipilia* extend southward to Thailand and Vietnam. In North America, there are no examples of such southern migration of temperate orchids in southern Florida and only a few in Mexico.

More primitive taxa are seen in eastern Asia (Chen, 1982). For example, a primitive genus *Tangtsinia*, possessing a regular perianth, a terminal stigma, and five staminodes, has been reported from southeastern Szechuan, where *Cathaya argyrophylla* Chun & Kuang also was found in 1958. Another primitive genus, *Archineottia*, is characterized by an incomplete column, exhibiting a terminal stigma and an erect stamen with a free filament attached to the back of the column. The columnar structure found in this genus and the allied *Neottia* is transitional from one form with a stamen not fully adnated to the style to another in which fusion is complete. The genus consists of four species, two in China and one each in Sikkim and northern India. Its ally, *Diplandrorchis*, possesses two stamens that are opposite the dorsal sepal and the median petal (lip) respectively. These orchids belong to the subtribes *Neottinae* and *Limodorinae*, both having suspensorless embryo and relatively large chromosomes, characters also found in the *Cypripedium* group and some other primitive taxa. Additionally, many other primitive genera such as *Apostasia*, *Cephalanthera*, *Sinorchis*, *Aphylorchis*, and *Pogonia*, also are found in eastern Asia.

DISTRIBUTION PATTERNS

The distribution patterns of the orchids indigenous to North America and eastern Asia can be divided into the following four categories:

Continuous distribution in the northern Pacific.

In this region, a few orchids are continuously distributed from Japan or northern China via the Aleutian Islands to North America. For example, *Orchis aristata* Fisch. occurs in Korea, northern Japan, Sakhalin, Kamchatka, the Aleutian Islands, and the Alaskan Peninsula (Fig. 1); *Platanthera hyperborea* (L.) Ldl. is found in northern Japan, Kamchatka, the Aleutian Islands, North America, Greenland, and Iceland; and *Cypripedium guttatum* Sw. var. *yatabeanum* (Makino) Pfitz. occurs in northern Japan, Kamchatka, the Aleutian Islands, and the Alaskan Peninsula (Fig. 2). However, attention is called to *Platanthera chorisiana* (Cham.) Rchb. f., which is distributed disjunctively in northern Japan, southern Sakhalin, and in the southeastern corner of Alaska and British Columbia, but is absent from the Alaskan Peninsula (Fig. 3).

Disjunctive distribution between eastern North America and eastern Asia. Within this category fall species pairs and individual genera. There are at least eight species pairs found in these two regions. They are similar in morphology and, in most cases, were formerly considered to be conspecific.

Cypripedium is a temperate genus of about 30 species. It is found largely in North America and eastern Asia, with two species extending to Europe. Two species pairs are distributed disjunctively in eastern North America and eastern Asia. *Cypripedium arietinum* R. Br. ranges from Illinois through New York, and Connecticut to Nova Scotia, southern Quebec, southern Ontario, and southern Manitoba; its Asian counterpart, *C. plectrochilon* Franch., occurs in Sichuan, western Hubei, and northwestern Yunnan (Fig. 4). Both species often grow in somewhat boggy and shady places. Another pair is of a slightly wider distribution: the American *C. reginae* Walt. extends as far south as North Carolina and Tennessee, whereas *C. flavum* Hunt & Summerh. is scattered from southeastern Tibet through Yunnan, Sichuan, and Hubei to southern Gansu (Fig. 5). The distribution patterns and environmental conditions of these two species pairs are similar, and both are rather primitive members in the genus. Apparently, the similarities between them are not fortuitous but rather indicate that they have shared a similar historical succession.

The genus *Listera* consists of some 30 species, all found in North America and Asia except for *L. ovata* (L.) R. Br. and *L. cordata* (L.) R. Br., which also extend their ranges to Europe. At least two disjunctive species pairs are generally rec-

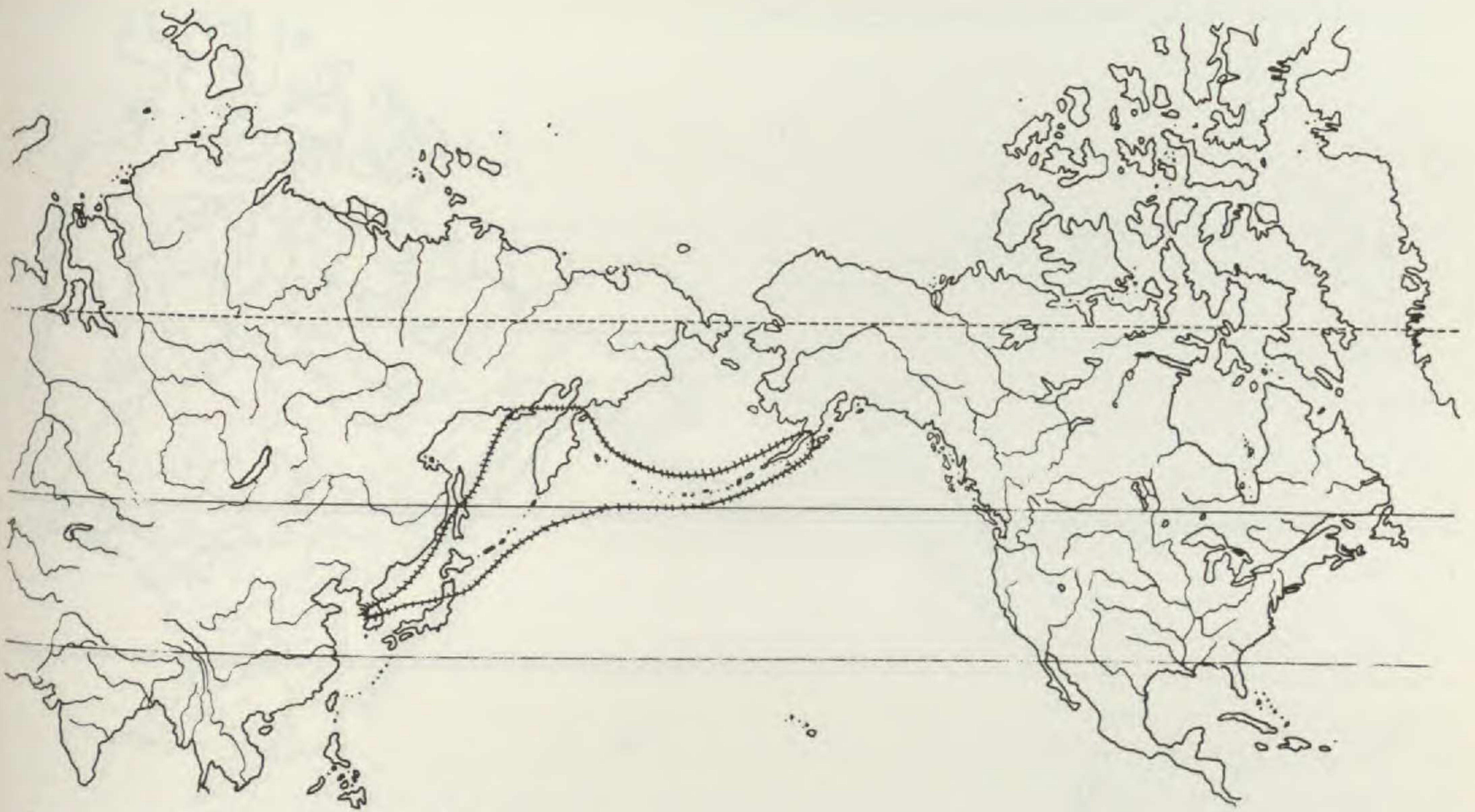


FIGURE 1. Distribution of *Orchis aristata*.

ognized: *L. australis* Ldl. and *L. japonica* Bl. and *L. smallii* Wiegand and *L. nipponica* Makino. *Listera australis* ranges from northern Florida and North Carolina northward to the southern tip of Quebec, whereas its counterpart is confined to Japan (Fig. 6). The other American species is narrowly distributed from North Carolina to

Pennsylvania, with its equivalent *L. nipponica* occurring in Japan and the far eastern part of the Soviet Union. *Listera nanchuanica* S. C. Chen, a western Chinese species, closely resembles *L. nipponica*. In addition, there are also some similarities between the American *L. borealis* Morong and the Japanese *L. yatabei* Makino, as well

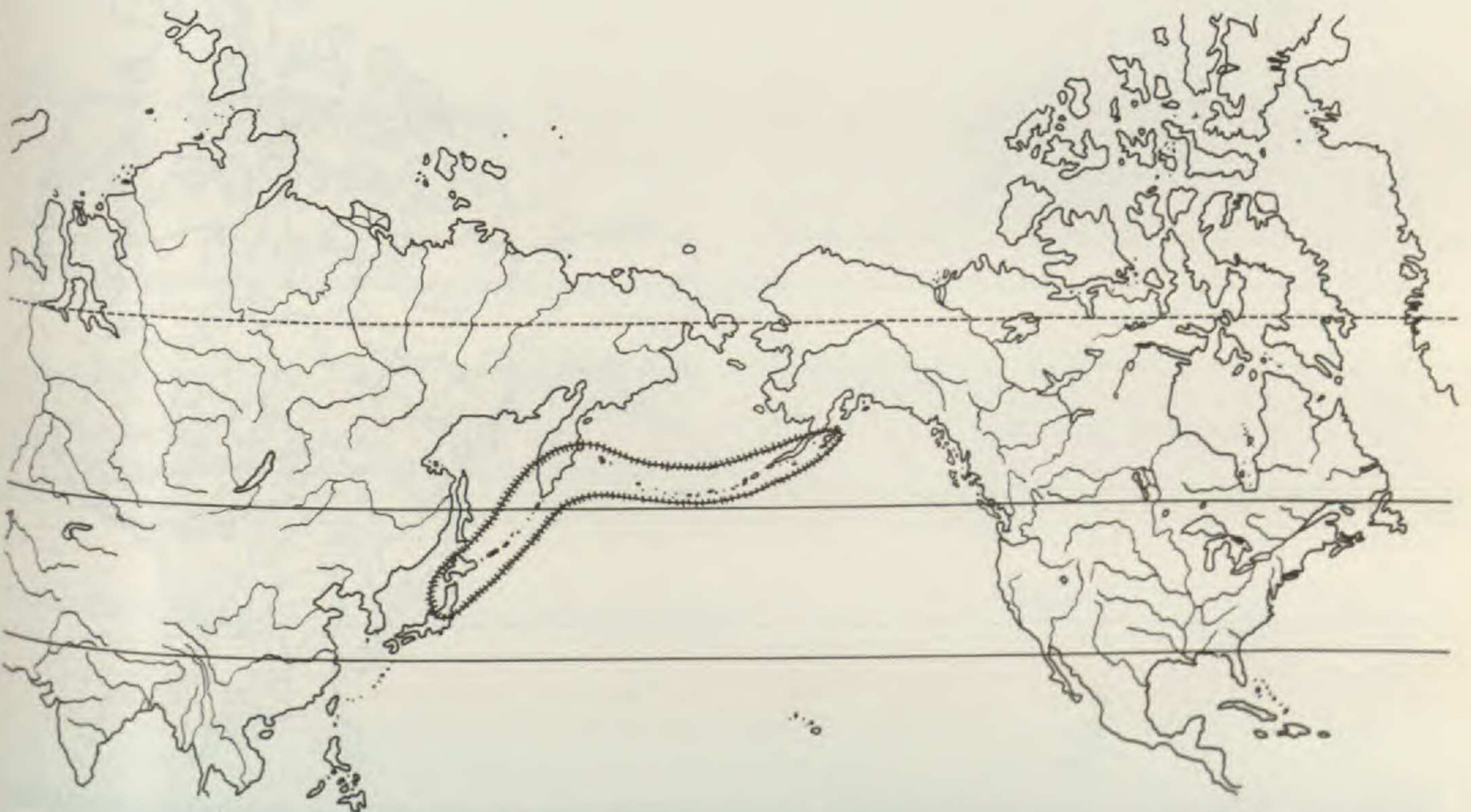


FIGURE 2. Distribution of *Cypripedium guttatum* var. *yatabeanum*.

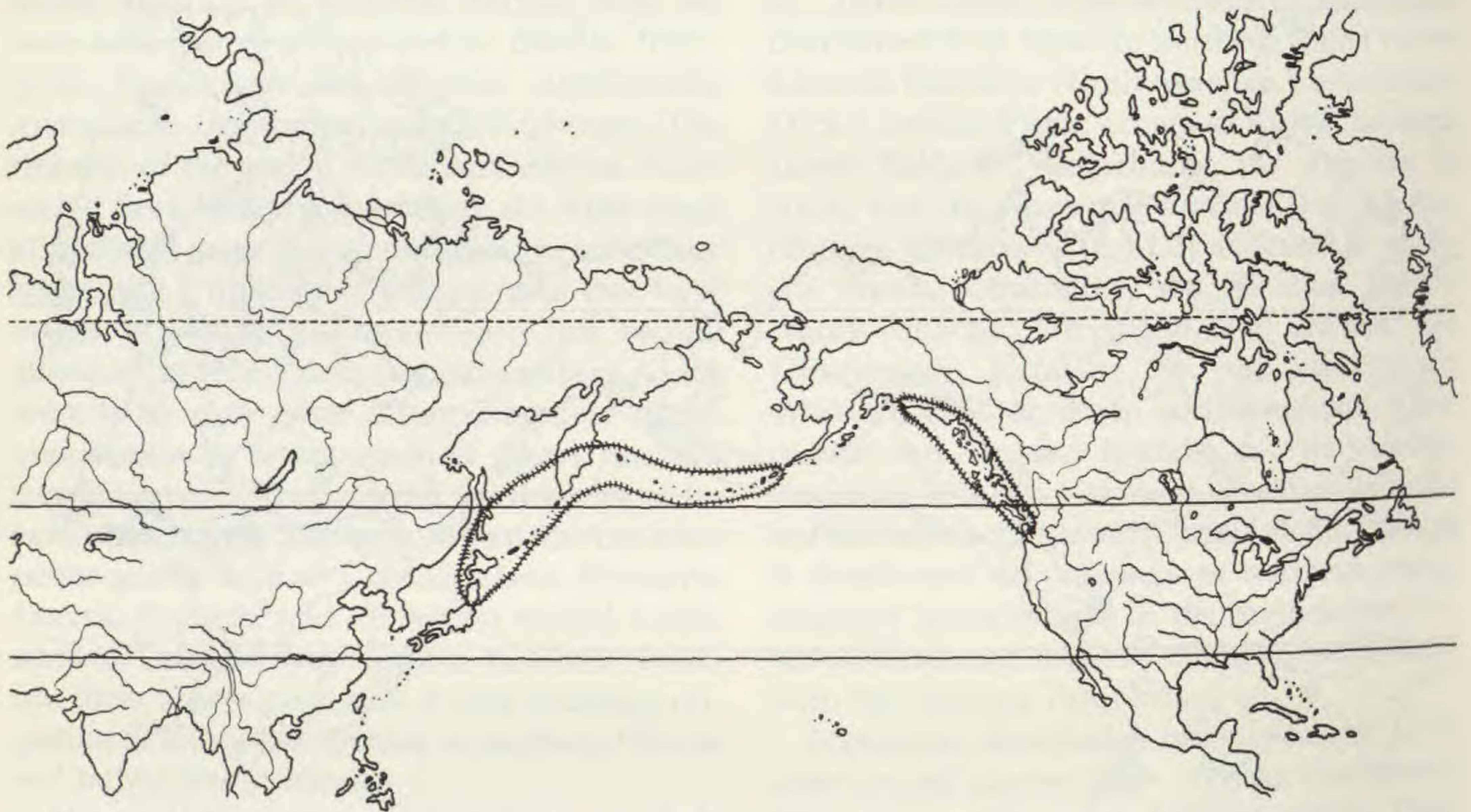


FIGURE 3. Distribution of *Platanthera chorisiana*.

as between the American *L. convallarioides* (Sw.) Nutt. and the Japanese *L. makinoana* Ohwi.

Liparis is a large genus of approximately 250 species. Its epiphytic members constitute the majority, and center in tropical Asia and Oceania. Two terrestrial species occur in temperate North

America, and about 25 species, mostly terrestrial, are found in eastern Asia. Among them, *L. lilifolia* (L.) L. C. Richard ex Ldl. and *L. makinoana* Schltr. are similar and constitute a species pair. *Liparis lilifolia* is found in eastern North America from Maine and Vermont along the At-

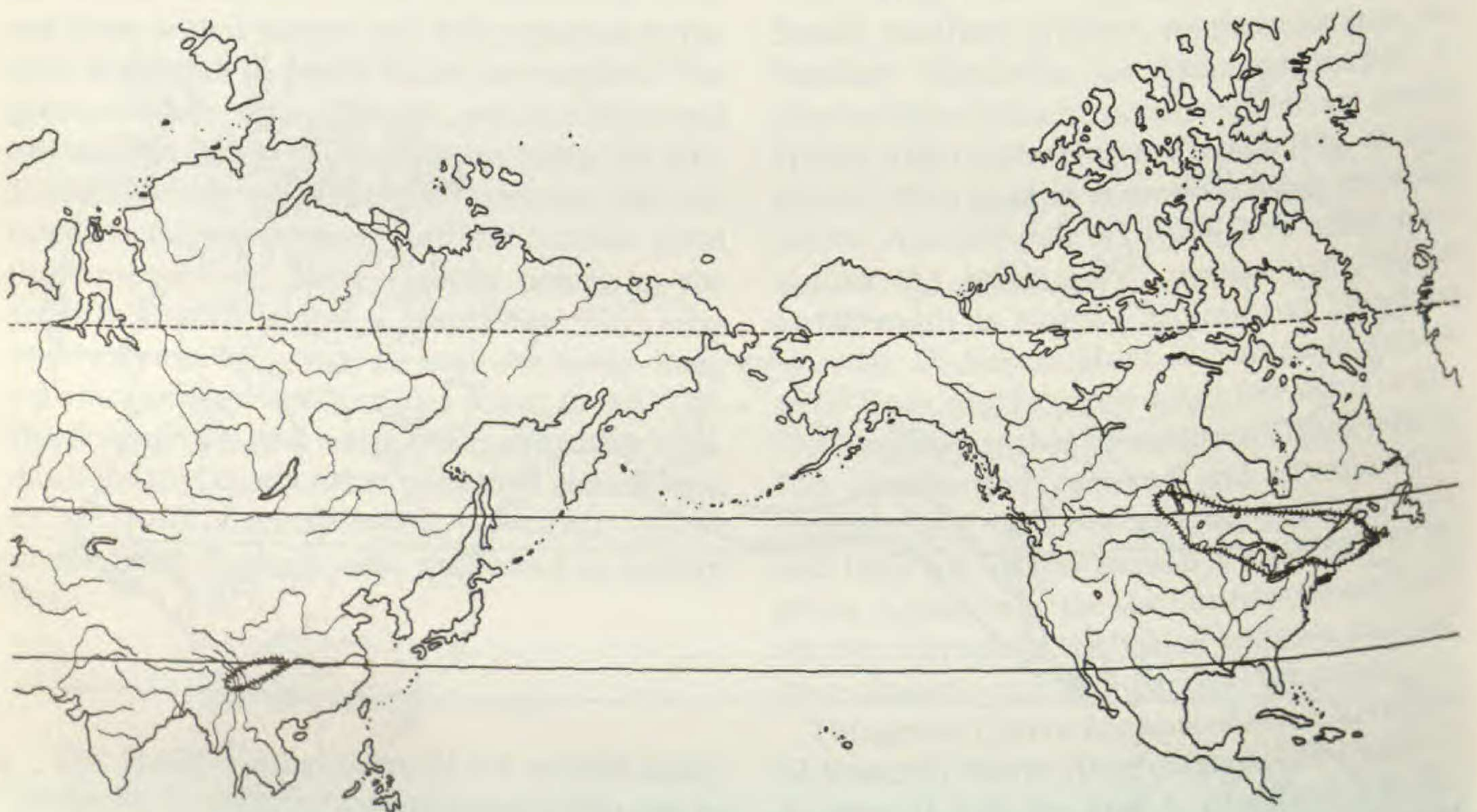


FIGURE 4. Distribution of the species-pair *Cyripedium plectrochilon* (eastern Asia) and *C. arietinum* (eastern North America).

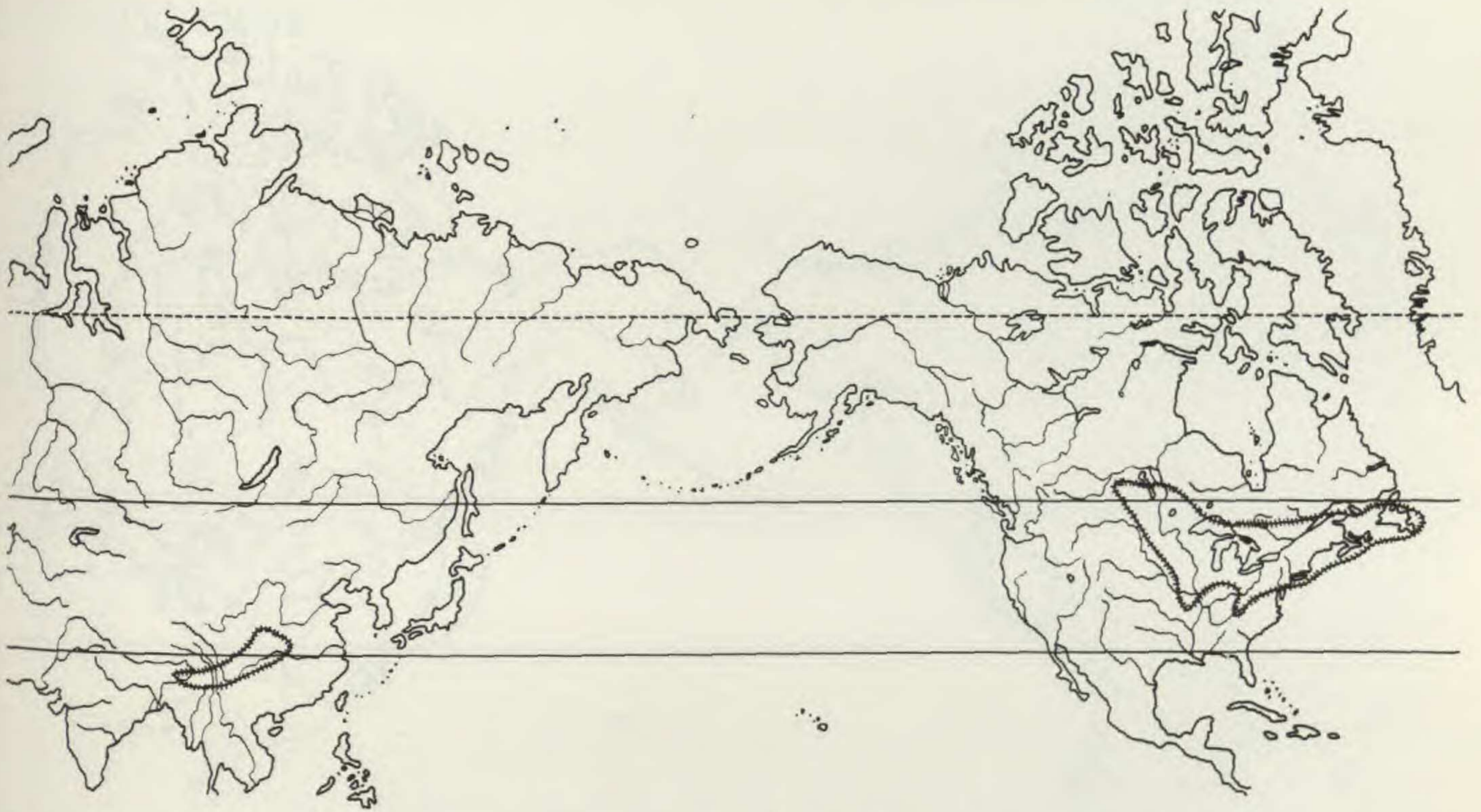


FIGURE 5. Distribution of the species-pair *Cypripedium flavum* (eastern Asia) and *C. reginae* (eastern North America).

lantic states southward to South Carolina, Georgia, and Alabama, and westward through the Central and Lake states to Wisconsin, Minnesota, Iowa, Missouri, and Arkansas, whereas its counterpart is confined to Japan (Fig. 8). Both

species are also similar to *L. pauliana* Hand.-Mzt., a species widespread to the south of the Yangtze River of China. Another interesting species is *L. loeselii* (L.) L. C. Richard, which is the only species in the family confined to North

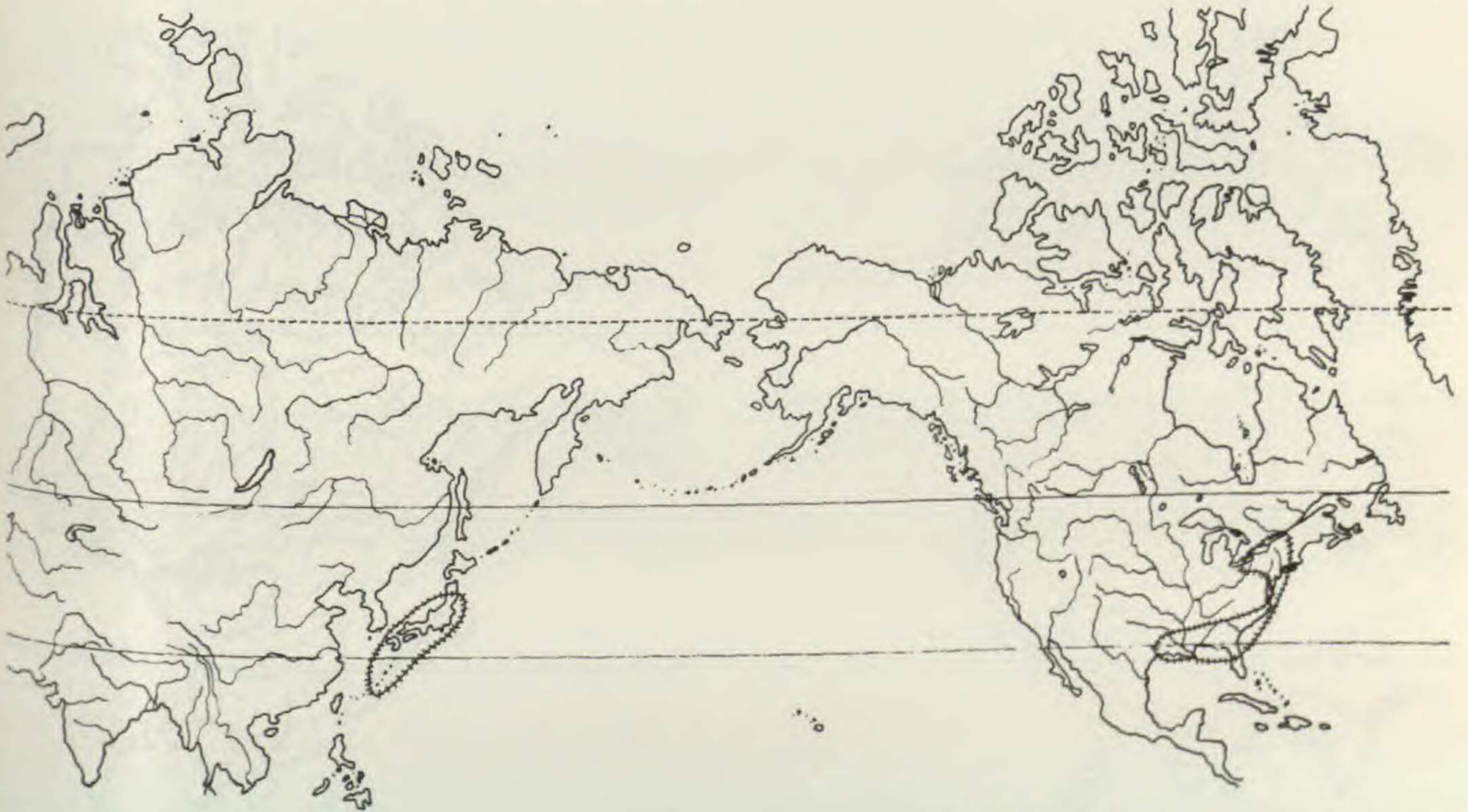


FIGURE 6. Distribution of the species-pair *Listera japonica* (eastern Asia) and *L. australis* (eastern North America).

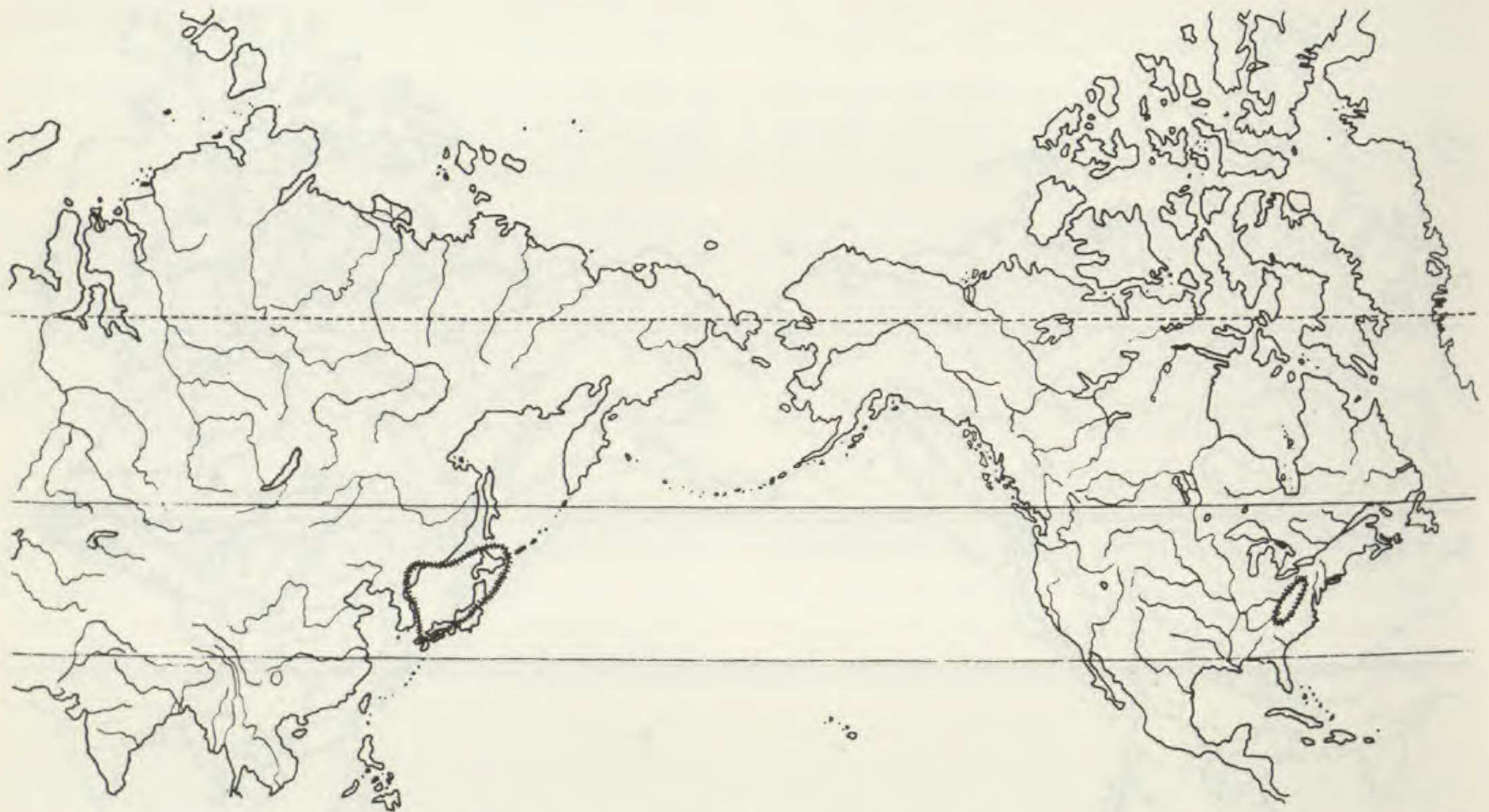


FIGURE 7. Distribution of the species-pair *Listera nipponica* (eastern Asia) and *L. smallii* (eastern North America).

America and western Europe. However, it shows some similarity to a Japanese species, *L. kumokiri* F. Maekawa.

Pogonia has an eastern Asia-eastern North American distribution. *Pogonia ophioglossoides* (L.) Ker-Gawl. is found in eastern North Amer-

ica from Newfoundland to Florida (Fig. 9). The other six species are in Asia, with their southern limits extending to Malaysia. *Pogonia ophioglossoides* is most similar to *P. japonica* Rchb. f., which is widely dispersed from the far eastern part of the Soviet Union and northeastern China

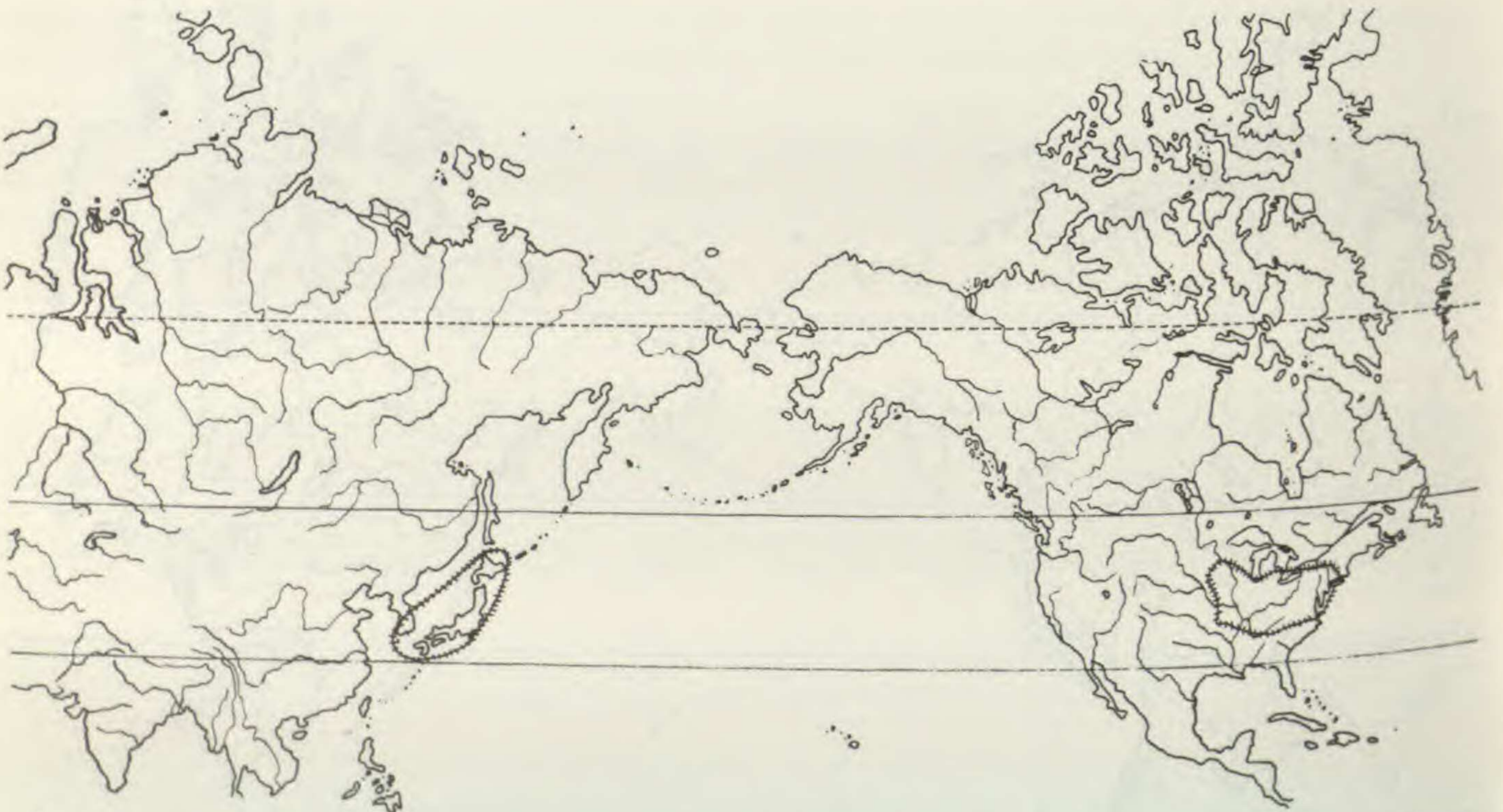


FIGURE 8. Distribution of the species-pair *Liparis makinoana* (eastern Asia) and *L. lilifolia* (eastern North America).

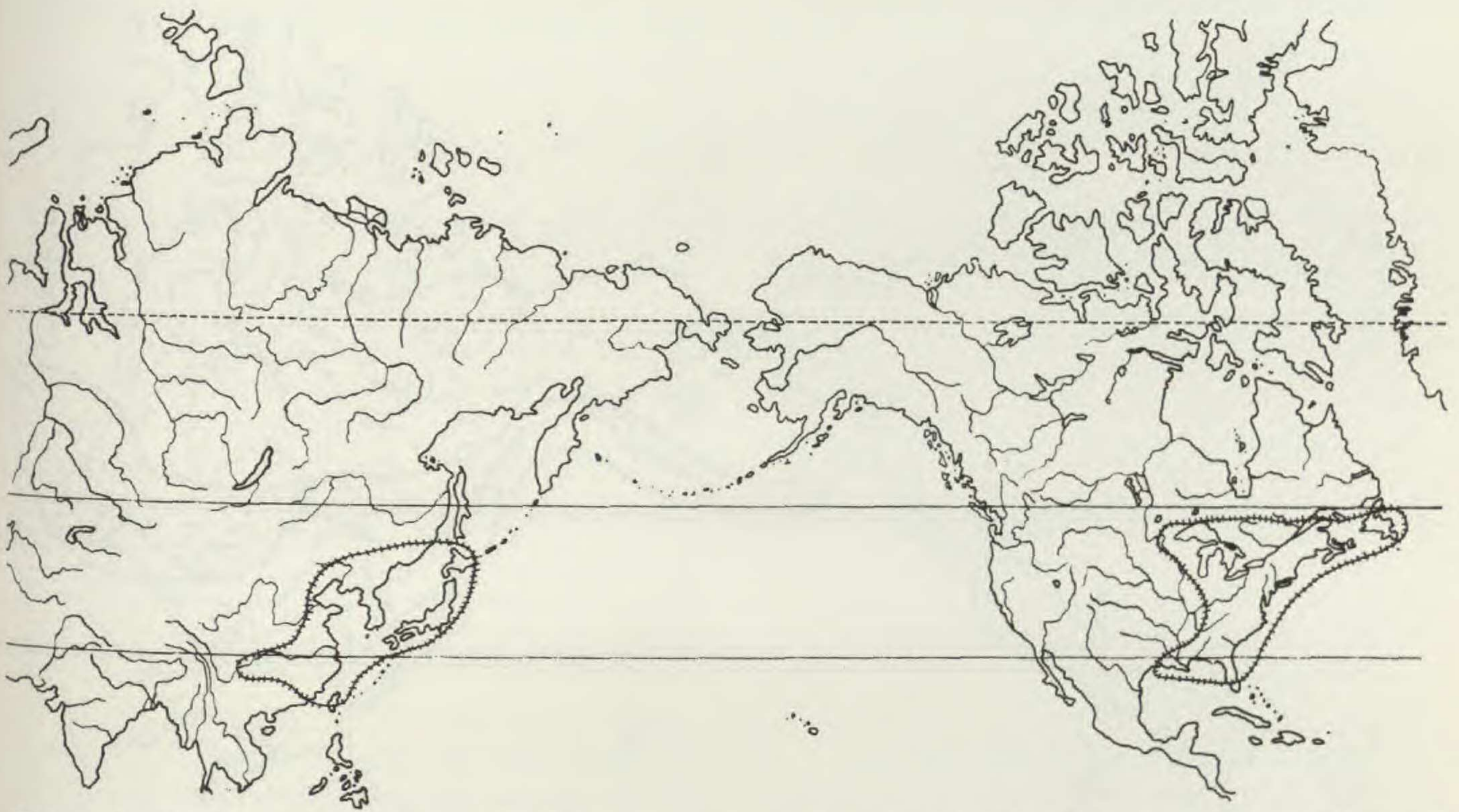


FIGURE 9. Distribution of the species-pair *Pogonia japonica* (eastern Asia) and *P. ophioglossoides* (eastern North America).

through Japan, southward to Jiangsi, Fujian, and Taiwan, and west to Sichuan and Kweichow in China (Fig. 9). *Pogonia* is a primitive genus possessing single pollen grains. In the New World, the genus has three allied genera, *Cleistis*, *Isotria*, and *Triphora*. These genera formerly were

included in *Pogonia*, from which they were separated mainly on the basis of more advanced compound pollen grains occurring in tetrads. In Asia, however, no closely allied genus to *Pogonia* is found.

Platanthera is of worldwide occurrence. Among

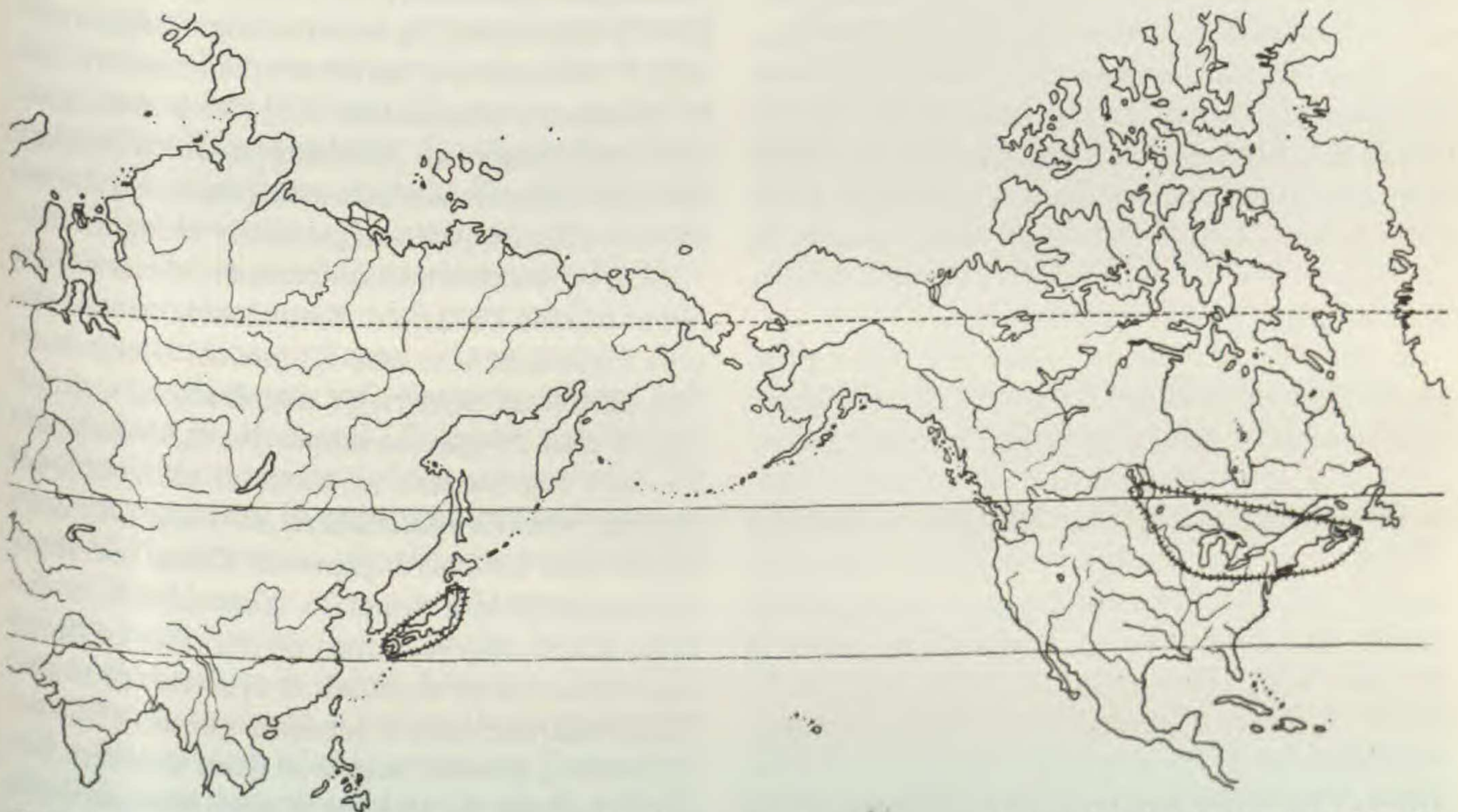


FIGURE 10. Distribution of the species-pair *Platanthera florentii* (eastern Asia) and *P. hookeri* (eastern North America).

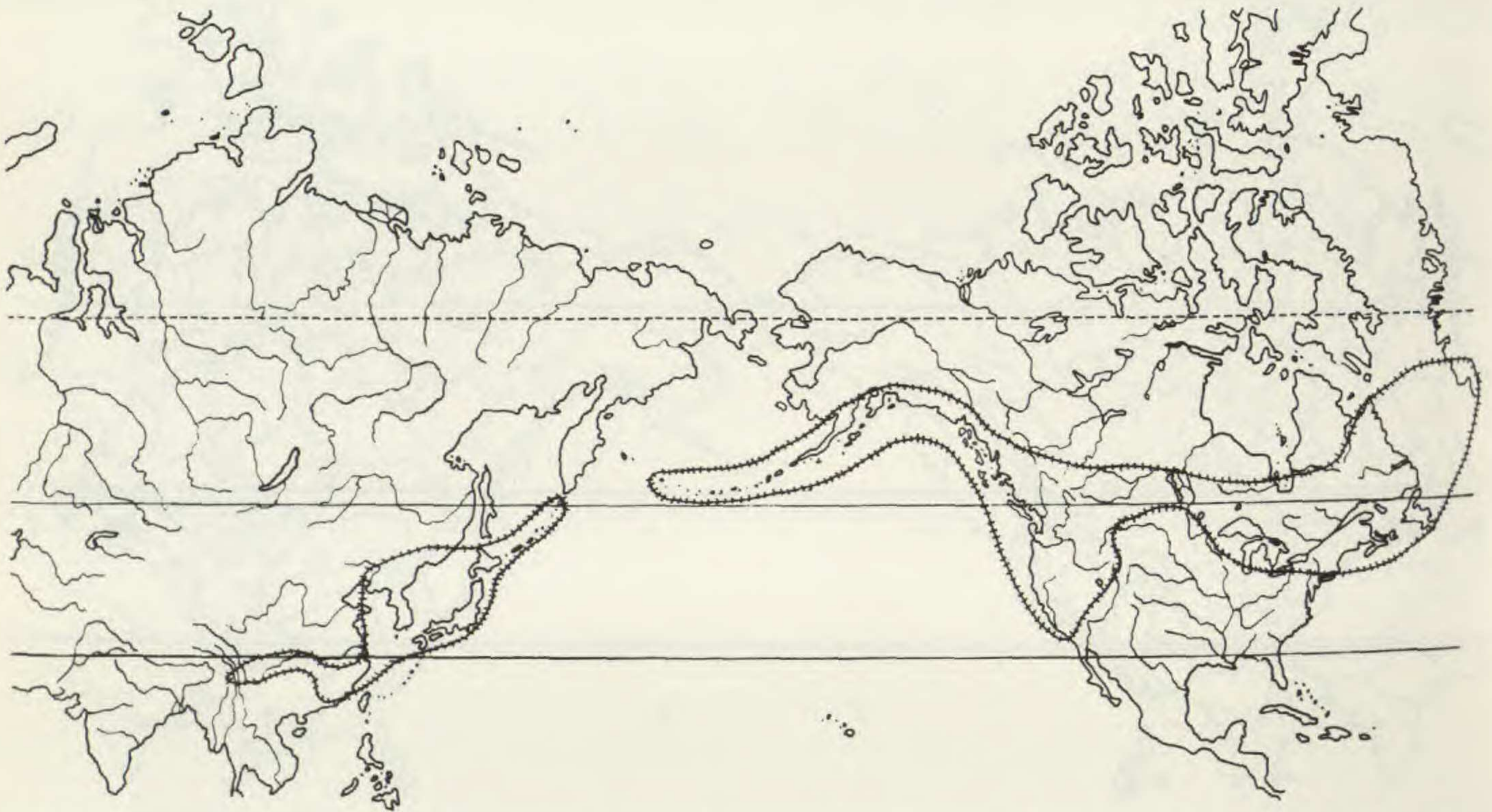


FIGURE 11. Distribution of the species-pair *Platanthera hologlottis* (eastern Asia) and *P. dilatata* (eastern North America).

its 200 species, about 40 are found in eastern Asia, and 36 in North America. The Japanese *P. florentii* Franch. & Sav. closely resembles the American *P. hookeri* (Torrey) Ldl., which occurs in southeastern Canada and the northeastern United States (Fig. 10). Of special interest is another species pair, *P. dilatata* (Pursh) Ldl. ex Beck and *P. hologlottis* Maxim. The former occurs in both eastern and western North America, including the Aleutian Islands, whereas the latter extends from the far eastern part of the Soviet Union southwestward to the Yunnan in China (Fig. 11). These species show a transition from the continuous distribution of same species to the disjunction of species pairs between eastern North America and eastern Asia.

In addition to *Pogonia*, there are three more genera that are confined to eastern North America and eastern Asia: *Tipularia*, *Arethusa* (*Eleorchis*), and *Aplectrum* (partly *Cremastra*). *Tipularia* is composed of five species: *T. discolor* (Pursh) Nutt. in southeastern North America, and *T. odorata* Fukuyama and *T. szechuanica* Schltr. in China (one in Taiwan, the other in Sichuan and Tibet) (Fig. 12). The map by Li (1952) includes *Tipularia camtschatica* Spreng., which is not a *Tipularia* but instead a *Platanthera*. The Asian species of this genus are more or less related. However, the American species

is rather different from the Asian species with respect to the fugacity of its solitary leaf prior to the appearance of the inflorescence. *Arethusa* and *Aplectrum* each contain two species that are disjunctively distributed in eastern North America and Japan. However, among specialists there are different opinions as to whether the Asian and American representatives are congeneric. Ohwi (1953) considered *Aplectrum unguiculatum* (Finet) F. Maekawa a member of *Cremastra*, and F. Maekawa established in 1935 a new genus *Eleorchis*, based on *Arethusa japonica* A. Gray. However, the close relationship between the two species of each pair are generally recognized.

Disjunctive distribution between western North America and Eurasia. Two closely related genera, *Cephalanthera* and *Epipactis*, demonstrate this particular pattern of distribution. Containing 14 and 20 species respectively, these genera are well represented in Eurasia, each with one species, viz. *Cephalanthera austinae* (A. Gray) Heller and *Epipactis gigantea* Dougl. ex Hook. in western North America. *Cephalanthera austinae* is the only saprophytic member of the genus, which is so unusual in appearance that A. Gray regarded it as a separate genus, *Chloraea*. *Epipactis gigantea*, scattered from southern British Columbia to Mexico is also unusual in appearance. Neither *Cephalanthera* nor *Epipactis*

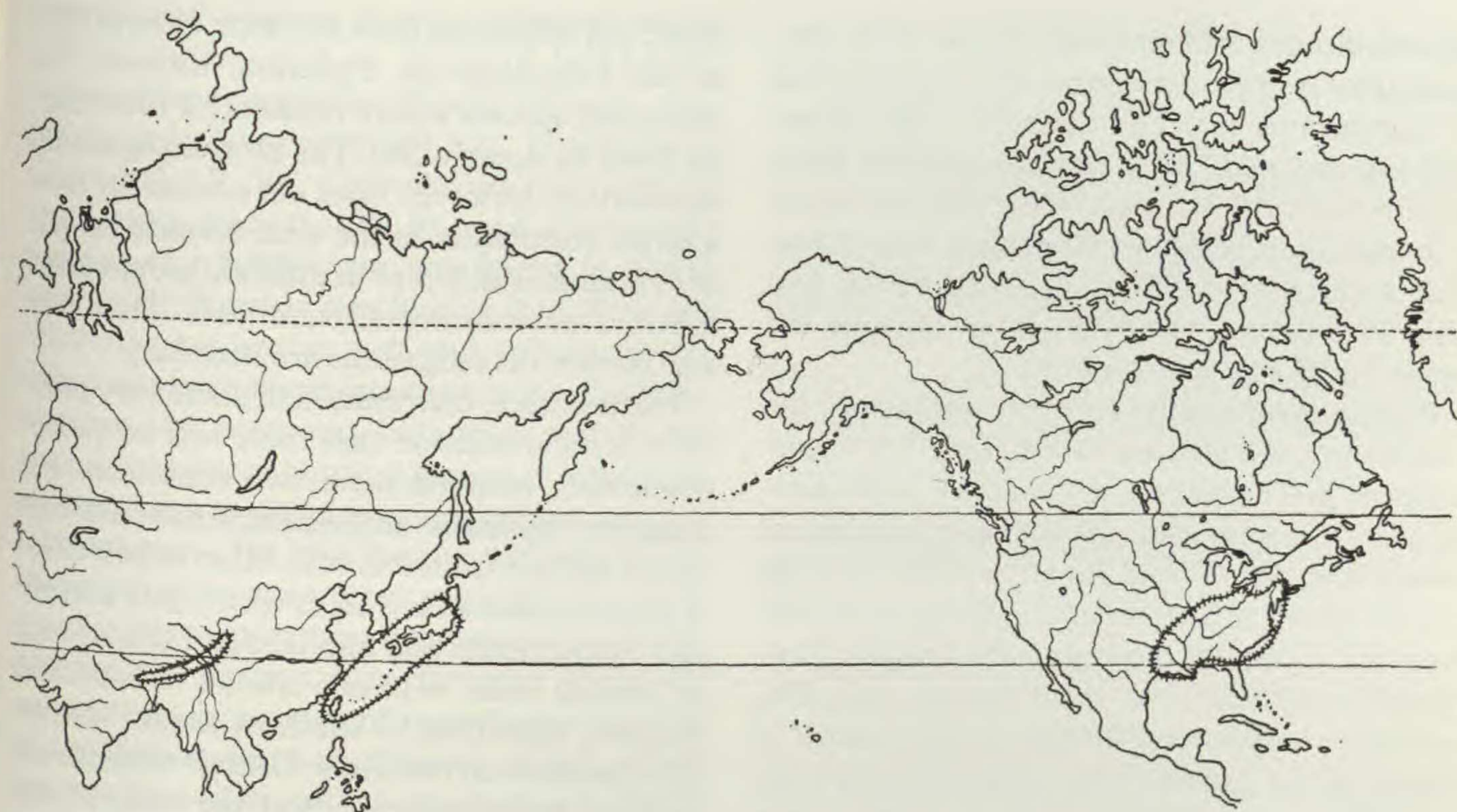


FIGURE 12. Distribution of *Tipularia*.

is found in eastern North America except *Epipactis helleborine* (L.) Crantz, which is a common species in Eurasia that was introduced into Canada some 100 years ago. The absence of these two genera in eastern North America could mean that they followed similar historical successions sharing similar ecological conditions.

Disjunctive distribution in the tropical Pacific. In southeastern North America and eastern Asia there are two orchid genera, *Tropidia* and *Erythrodes*, that are disjunctively distributed. *Tropidia* consists of about 20 species, including a single New World species, *T. polystachya* (Sw.) Ames, extending from southern Florida, Mexico, and Central America to the northern end of South America. The remaining members are all tropical Asian and Oceanian, with their northern limits of distribution in Japan (*T. nipponica* Masam.) and Sichuan of western China (*T. emeishanica* K. Y. Lang). *Tropidia polystachya* is different from the rest of the genus except for its slight similarity in habit and inflorescence to those of *T. nipponica*. *Erythrodes* is essentially a New World genus of some 100 species. *Erythrodes querceticola* (Ldl.) Ames is the only species that occurs in North America, extending from Florida to South America. In tropical Asia only a few species of this genus are found, two of which extend northward to China: *E. chinensis* (Rolfe) Schltr. of Yunnan and Kwangdong

and *E. latifolia* Bl. of Taiwan and Malaysia. Neither of these genera is found in Africa.

DISCUSSION AND INTERPRETATION

It is evident from the foregoing data that the distribution of Orchidaceae between the two continents follows the general rule, although it is an advanced family.

All taxa mentioned above are terrestrial, belonging to different groups, most of which are less advanced members of the family. No epiphytic orchid shows such a pattern of distribution. Although the genus *Bulbophyllum* has a single species occurring in southern Florida (Luer, 1972), and several in eastern Asia, little similarity can be found between them. As a pantropical genus, *Bulbophyllum* consists of more than one thousand species, all of which are epiphytic.

The distribution of the species pairs on two continents often show some similarity and correlation among them. For example, the American species *Pogonia ophioglossoides* is widespread and *Listera smallii* is of local occurrence. Similarly, their Asian counterparts *Pogonia japonica* and *Listera nipponica* are widely and narrowly distributed, respectively. Probably this is due to similar ecological preference and genetic character. However, the American species often show a wider range of distribution and reach

higher latitudes, whereas their Asian allies generally grow at higher elevations. Two species pairs of *Cypripedium* are good examples. The ranges of *C. reginae* and *C. arietinum* extend as far north as 50°N in North America, where they are found at an elevation below 1,000 meters; their Asian counterparts are confined to south of the Qin Ling Mountains (33°–34°N) at an altitude between 1,850 and 3,700 meters.

Phytogeographically, Japan is significant; the aforementioned taxa are found except for *Cypripedium plectrochilon*, *C. flavum*, and *Erythrodes*. In some cases, species have continuous ranges that extend from Japan or China through coastal areas and continental islands to North America. Examples include *Orchis aristata*, *Cypripedium guttatum* var. *yatabeanum*, and *Platanthera chorisiana*, although the last species is absent in the Alaskan Peninsula, showing a degree of disjunction in its range. A highly interesting pattern of distribution is exhibited by the species pair *Platanthera dilatata* and *P. hologlottis*, which seem to have been differentiated more recently. Should further climatic changes take place causing their extinction in northwestern North America and northeastern Asia, their distribution would approach that of *Cypripedium reginae* and *C. flavum*.

Thus there is a series of transitions in distributional types; *Orchis aristata* type (continuous distribution in the northern part of the Pacific at the species level); *Platanthera chorisiana* type (distribution somewhat disjunctive in the northern part of the Pacific at the species level); *Platanthera dilatata*–*P. hologlottis* type (species pairs between North America and eastern Asia); *Listera australis*–*L. japonica* type (species pairs between eastern North America and western China); *Tipularia* type (disjunctive distribution between eastern North America and eastern Asia at the generic level); and *Tropidia* type (disjunctive distribution in the tropical Pacific at the generic level). It might be assumed from these types that the migration of orchids between these two continents must have taken place repeatedly in different geological times, probably via coastal areas and continental islands of the northern Pacific. The *Orchis aristata* type and the *Platanthera chorisiana* type must represent more recent migration. Slightly earlier would be those of species pairs, such as the *Platanthera dilatata*–*P. hologlottis*, the *Listera australis*–*L. japonica*, and the *Cypripedium arietinum*–*C. plectrochilon*

types, but migration does not seem to be as early as the Paleogene. In *Tipularia*, however, the American species shows remarkable dissimilarity from its Asian allies. The morphological differentiation, however, does not necessarily show a direct correlation to the time because the rate of evolution is different in different groups under different environmental conditions. More data and further investigations are necessary.

Furthermore, distribution of some very primitive orchids indicate that there was an ancient connection between these two continents. For instance, *Apostasia* and *Selenipedium* are both relicts and are related to each other in possession of a three-celled ovary, seeds with highly sclerotic and opaque testa, and habits. *Apostasia* is found in tropical Asia, with one species *A. nipponica* Masam., extending to southern Japan, whereas *Selenipedium* is confined to Central America and northern South America. Both the mode of their differentiation and whether or not they are monophyletic is still unknown. However, it seems possible that some subtropical orchids, such as *Tropidia* and others, had migrated through Beringia. During the Eocene, as pointed out by J. A. Wolfe (1972), tropical forests did exist in Alaska. At the same time, the subtropical zone had reached as far north as 42°N in China (Hsü & Li, 1980), and subtropical forests seem to have covered nearly the whole of Japan (Tanai, 1972). Such a climate lasted for a long time until the second half of the Pliocene.

The dissimilarity between orchid floras of western and eastern North America is notable. In western North America there are only ten genera, of which only *Cephalanthera* and *Epipactis* are absent from the East Coast. The flora of California, as pointed out by Raven and Axelrod (1978), is characterized by a high degree of endemism. No exception is found in Orchidaceae. For example, *Cephalanthera austinae*, *Cypripedium californicum* A. Gray, and *Platanthera* sect. *Piperis* all are very distinct taxa, to which no close allies are found in eastern North America and Eurasia.

There is little indication of more recent interchange of orchids between western Europe and North America, although it is generally recognized that, during the Late Cretaceous and early Tertiary, European floras were similar to that of eastern North America, but not to that of Asia (Hallam, 1981). Only one species, *Liparis loeselii*, is exclusively indigenous to eastern North

America and western Europe, whereas many Eurasian species, such as *Epipactis helleborine*, *Cephalanthera longifolia* (Huds.) Fritsch, *Epipogium aphyllum* (Schmidt) Sw., *Gymnadenia conopsea* (L.) R. Br., *Cypripedium macranthum* Sw., *Listera ovalis* (L.) R. Br., and *Neottianthe cucullata* (L.) Schltr., are not found in North America. It deserves mentioning that *Epipactis helleborine* has grown well and spread rapidly since it was introduced into eastern North America some 100 years ago, indicating that its absence from eastern North America is not due to ecological but to phytogeographical causes.

In summary, the distribution patterns of Orchidaceae, as in most other angiosperms, show close floristic relationships between eastern North America and eastern Asia. Between these two regions there is a series of transitional patterns of distribution from continuous ranges of the same species to disjunctive ones of closely related species pairs and species. It is rational to interpret that the disjunctive distribution between eastern North America and eastern Asia was realized as the result of the migration via Beringian link and the coastal areas as well as through the continental islands, although these were not necessarily the only migration routes. From these data, of course, it seems to be of little significance to assume the time of their interchange, the origin, and the direction of migration, because there are only few fossil records available for the Orchidaceae (only *Protorchis* from the Eocene in Europe is considered to be credible, and the others such as *Paleorchis* and *Orchidacites*, are more or less doubtful), and their genetic relationships are not clear. As an advanced family, however, such data would be of some help in elucidating certain facts concerning the floristic relationships between temperate North America and eastern Asia.

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